Processing spatial information in the sensorimotor branch of the visual system

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Abstract

We distinguish two representations of visual space: a cognitive representation drives perception, and a sensorimotor representation controls visually guided behavior. Spatial values in the two representations are separated with the Roelofs effect: a target within an off-center frame appears biased in a location opposite the direction of the frame. The effect appears for a verbal measure (cognitive) but not for a jab at the target (sensorimotor). A 2-s response delay induces a Roelofs effect in the motor measure, showing the limit of motor memory. Motor error is not correlated with reaction time. Subjects could strike one of two identical targets, a process involving choice, without intrusion of a Roelofs effect, showing that the sensorimotor system can use its own coordinates even when a cognitive choice initiates the motor processing. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Evidence from many sources is converging on the concept of a visual system with two distinct branches. The systems share a common 'early vision' input, differentiating only later in the processing stream. One system, specialized for perception, will be identified as the 'cognitive' system. Its processing results in all the richness and variety of visual experience.

The other system, identified here as 'sensorimotor' following the terminology of Paillard (1987, 1991), is specialized for visually guided behavior. It can control motor activity even when adequate information for localization is not available in the cognitive system. A subject need not be aware of the processing of visual information, i.e. need not perceive it, in order to jab, hit, grasp, or otherwise interact with a visually present object.

Some of the earliest evidence for this idea came from rodents, where lesions of the superior colliculus led to the inability to run a maze, combined with preserved discrimination abilities in pattern discrimination. In other animals, visual cortex lesions disturbed pattern discrimination without interfering with maze-running ability (Schneider, 1969). This forebrain–midbrain distinction seems to have changed over the course of evolution, as both the pattern recognition and the spatial orientation branches became corticalized into cognitive and sensorimotor systems respectively in primates (Trevarthen, 1968).

According to this conception, early transformations of visual information take place in a unified system. Then, from a common origin in primary visual cortex, information flows to two distinct branches of the visual system. The cognitive system in primates follows a course into the temporal lobe, while the sensorimotor system extends to posterior parietal areas, creating an anatomical dissociation between cortical areas coding visual experience and areas handling the pickup of the information that controls visually guided behavior. Experimental lesions in primates reveal this dissociation between cognitive functions in a temporal brain region and sensorimotor functions in a parietal region. Monkeys with lesions of the inferior temporal cortex have

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difficulty in performing visual discriminations (Pribram, 1971), but have good hand–eye coordination, while animals with posterior parietal lesions have good discrimination skills but are clumsy and uncoordinated in reaching and grasping.

2. Neurophysiology in human patients

Human neurological patients show patterns similar to those of lesioned. monkeys. Some patients show the symptom of visual ataxia, an inability to reach for and grasp objects appropriately despite being able to identify them. The deficit is not a general damage to motor ability, for grasp that is not guided by vision can remain normal. In ataxia patients, information in the perceptual pathway is not available to control accurate grasping and reaching. These patients have damage to the sensorimotor system.

Another, less common group of patients has difficulty with perception and object identification, but can reach for and grasp objects accurately even though their properties cannot be identified. One such patient cannot identify the orientation of a slot cut into a disk held before her. But when asked to extend her flattened hand through the slot, she rotates her hand appropriately (Milner & Goodale, 1995). Such patients have damage to the cognitive system. This is a demonstration of a sensorimotor pathway possessing accurate information that is not available to perception. Here the definition of perception will be limited to perceptual experience, events that a subject can remember and talk about; it does not include information pickup without experience.

Neurophysiological evidence has also implicated a parietal pathway, specifically in the posterior parietal region, in visually guided pointing behavior. This region is activated (among other regions) in PET scans collected during visually guided pointing (Lacquaniti et al., 1997).

Clinical studies have the limitation that the patients' brains may become reorganized as a result of their pathology. We cannot be sure that functions that are distinct in brain-damaged patients or lesioned monkeys are also distinct in normal brains, for the brain may erect a 'firewall', dividing a normally unified system so that at least part of normal function can continue despite damage to another part of the system. To know how these two pathways normally operate and cooperate, they must be studied in normal humans. This has become possible recently with the development of psychophysical methods that can isolate the two pathways and measure separately the spatial information in each representation. Some of these attempts have been successful, and others less so.

3. Normal humans

Common sense tells us that one must accurately perceive an object's location and properties to interact effectively with it. This intuition is in error, however: there are now numerous experimental designs in which humans produce effective motor behavior despite inadequate or erroneous perceptual information. Perception is not required to visually guide an action. Early experiments on separation of cognitive and sensorimotor systems showed that normal subjects were unable to perceive jumps of targets that take place during saccadic eye movements (a cognitive-system function). But the subjects could still point accurately to the new locations of the same targets (a sensorimotor-system function), even if their pointing movements were controlled open-loop (Bridgeman, Lewis, Heit, & Nagle, 1979). This showed that information about the new location of the target was accurate, but was not available to perception.

A more rigorous method of separating cognitive and sensorimotor systems is by double dissociation, introducing a signal only into the sensorimotor pathway in one condition and only into the cognitive pathway in another (Bridgeman, Kirch, & Sperling, 1981). If each manipulation can be performed without affecting the representation in the other pathway, then they must store spatial information independently. A fixed target was projected in front of a subject, with a frame surrounding it. When the frame was displaced left or right, subjects had the illusion of stroboscopic induced motion — the target appeared to jump in the opposite direction. Target and frame were then extinguished, and the subjects pointed to the last target position. They pointed to the same location despite the induced motion. The illusion did not affect pointing, showing that the displacement was coded only in the cognitive system.

In another condition we inserted displacement information selectively into the sensorimotor system by nulling the cognitive signal. Each subject adjusted the real target jumps until the target appeared stationary, with a real displacement in phase with the background jump equaling the induced displacement out of phase with the background. Thus, the cognitive pathway specified a stable target. Nevertheless, subjects pointed in different directions when the target was extinguished in the left or the right positions, showing that the difference in real target positions was still represented in the sensorimotor pathway. This is a double dissociation because in the first condition the apparent target displacement affected only the cognitive measure, while in the second condition the real displacement affected only the sensorimotor measure.

If a moving target is sampled at different times for different functions, apparent dissociations might result

even though a unified visual representation underlies each function. Recently, other methods have been developed to test dissociations of cognitive and sensorimotor function without possible confounding effects of motion, by using static illusions. One method is based on the Ebbinghaus illusion, also called the Titchner circles illusion. A circle appears to be larger if it is surrounded by smaller circles than if it is surrounded by larger circles. Aglioti, DeSouza and Goodale (1995) exploited this illusion by making the center circle into a three-dimensional (3D) poker chip-like object and asking subjects either to judge the size of the circle or to grasp it. The grasp was adjusted closer to the real size of the circle than to its illusory size. Subjects were able to see their hands, however, so it is possible that they adjusted their grasp not to the non-illusory true size of the circle, but to the visible error between the grasp and the edge of the circle. The adjustment did not occur until just before the movement was completed, nearly 2 s after it started.

Recognizing this problem, Aglioti et al. (1995) noted that calibration of grip aperture has been shown to be largely refractory to visual information available during a movement, relying instead on motor programming that occurs before the movement begins. The experimental support cited for this open-loop property, however, concerns movements to targets without illusory size modifications, so that visual recognition of grasp error and subsequent correction would not occur. The movements can be controlled open-loop because no correction is necessary. In a subsequent experiment that avoids the feedback confound, Haffenden and Goodale (1998) measured the Ebbinghaus illusion either by asking subjects to indicate the apparent size of a circle or to pick it up, in both cases without vision of the hand or the target. The illusion appeared for the estimations, but was much smaller for the grasp, indicating that the sensorimotor system was relatively insensitive to the illusion.

There are several caveats to this result. First, binocular information appears to be necessary for the sensorimotor system to overcome the illusion (Marotta, DeSouza, Haffenden, & Goodale, 1998). Second, static size illusions appear to influence the predicted weight of an object, measured by the force used to lift it, even when the illusions do not affect size of grip aperture (Brenner & Smeets, 1996). Another experiment contrasting grasp and perception, using the Müller–Lyer illusion, showed that while the illusion is smaller when measured with grasp than with perception, there is some illusion under both conditions (Daprati & Gentilucci, 1997). Again, relatively slow grasp movements may be responsible, and vision of both hand and stimulus was allowed.

In summary, experiments in normal subjects suggest behavioral evidence for a distinction between process-ing in two visual streams, but we know very little about processing in the sensorimotor pathway. With the exception of the saccadic suppression and the induced motion methods reviewed above, all of the methods address the properties of objects rather than their locations. A method was needed to examine egocentric spatial localization in cognitive and sensorimotor modes in normal subjects, without possible confounds of motion and position.

4. Static cognitive and sensorimotor measures of position

Another approach has produced large and consistent contrasts between cognitive and sensorimotor systems, differentiated by response measure. The dissociation is based on another perceptual illusion, the Roelofs effect: if a rectangular frame is presented off-center, so that one of its edges is directly in front of the subject, that edge will appear to be offset in the direction opposite the rest of the frame. A rectangle presented on the left side of the visual field, for example, with its right edge in the center, will appear less eccentric than it is, and the right edge will appear to be to the right of the subject's center (Roelofs, 1935).

We have extended and generalized this phenomenon to apply it to the study of the two visual-systems theory. First, the frame need not have one edge centered in front of the subject; illusions of location occur whenever the frame is presented asymmetrically in the visual field. Second, if a target is presented within the offset rectangle, the target's location tends to be misperceived in the direction opposite the offset of the frame. Misperception of frame position induces misperception of target position; this is an induced Roelofs effect, but will be called simply the Roelofs effect here.

Roelofs effects can be observed reliably if subjects describe the target's position verbally, a task that addresses the cognitive system. If their task is to point to the target as soon as it disappears from view, however, they are not affected by the frame position. This task addresses the sensorimotor system. Motor behavior for many subjects remains accurate despite the perceptual mislocalization (Bridgeman, 1991).

The result is different if a delay is imposed between the target disappearance and motor response. After a delay of 4 s most subjects point in directions that are biased by the cognitive illusion. This result was interpreted as a consequence of loss of veridical information available only to the sensorimotor system: having lost the accurate representation in that system, subjects must import the remembered spatial information from the perceptual system. In the process they import the illusion as well, and the illusion serves as a marker for the source of the information (Bridgeman, Peery, &

Anand, 1997). Ability to transfer spatial information from one system to another under some circumstances does not mean that the two systems are really one, any more than the ability of two people to communicate under some circumstances would mean that they are really one. Further, information transfer seems to go in only one direction, from cognitive to sensorimotor representations. Sensorimotor system information cannot be used to make verbal judgments, even when it is accurate and the verbal information is not.

A difficulty in interpreting these experiments was that not all subjects showed the predicted pattern. In the pointing condition, accessing the sensorimotor system, half of the subjects showed no Roelofs effect in the no-delay condition while the other half showed a robust effect. The distribution of effect sizes was bimodal: some subjects showed no sign of the Roelofs effect while others showed a large and significant effect. This inconsistency was interpreted with the assumption that the latter subjects had already shifted to a memory mode, and had to import the cognitive system's representation to control their pointing. To test this interpretation, we predicted that imposing a delay would cause the Roelofs effect to reappear in the motor measure for the other subjects as well. Indeed, with a 4-s delay nearly all subjects showed the predicted Roelofs effect in pointing.

In our earlier studies, half of our subjects showed a Roelofs effect with a motor measure and half did not, even with no delay between stimulus offset and response. Why did some subjects switch to importing spatial information from the cognitive system? The tendency to use cognitive spatial values to do a sensorimotor task may originate from the control of the pointing task. In aiming at a target, the subjects indicated their opinion about target position to the experimenter, much as the subjects of Haffenden and Goodale (1998) indicated with their fingers the perceived size of a disc. Though the act in our case is isornorphic with stimulus position, it is a communicatory act, and might be closely linked to cognitive representations. An alternative is to require an instrumental act, in which a subject must do something to the world rather than simply indicate a position to another person.[1] Behavior with a purely instrumental goal might be different from behavior with a communicatory goal, even if both the stimuli and the motor movements themselves are identical.

Thus in the current experiments we asked subjects to jab a 3D target object, pushing it backward and making a clicking noise. Their intention was not to communicate anything, but only to do something to the world. With this improvement in our measurement techniques

we achieve a cleaner separation of cognitive and motor systems. With a quick jab at a 3D target, rather than a pointing motion, almost all subjects show independence from Roelofs effects in immediate action, along with the previously observed robust Roelofs effects in verbal estimation of position.

Because this series of experiments follows up on earlier studies (Bridgeman et al., 1997), we were able to take advantage of the results of those studies to improve our experimental design. In the earlier data nearly all of the variance in responses as a function of target position was accounted for by a linear regression, so in the current experiments we did not need to present five target positions: two target positions would give us the same information, and allow us to increase the number of trials per condition. In measuring the effects of delay in the earlier experiments we had begun with a 4-s delay, but we found that almost all subjects had already lost the information in the sensorimotor pathway by that time. Here we investigate shorter delays to determine the duration of the sensorimotor system's memory for position.

Using these improved techniques, we begin the job of characterizing the psychophysics of the sensorimotor system.

5. Experiment 1

Since previous work had shown the sensorimotor representation to be definable with no delay, but to have largely disappeared with a 4-s delay, this experiment investigates the effects of shorter delays to define the effective duration of information storage in the sensorimotor representation.

5.1. Method

5.1.1. Subjects
Nine University of California undergraduates participated in the experiment, all right-handed with normal or corrected-to-normal visual acuity. Four were male and five female.

5.1.2. Apparatus
Subjects sat with heads stabilized before a white hemicylindrical screen that provided a homogeneous visual field 180° wide × 50° high. A lever box located in front of the screen presented five white levers, each 1.8° wide, spaced 2.5° apart center-to-center (Fig. 1). The center lever, marked with a black stripe, functioned as the target. Each lever was hinged at its base and spring-loaded. It activated a microswitch when pushed backward by 5 mm. A long black baffle hid the microswitch assembly without revealing the position of the lever array. In the motor condition, the task was to

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[1] We thank Prof. Josef Pemer, Salzburg, for this suggestion.

jab the black target stripe rapidly with the right forefinger. The remaining levers served to record the locations of inaccurate responses.

A rectangular frame 38° wide × 1° in line width was projected, via a galvanic mirror under computer control, either centered on the subject's midline, 6° left, or 6° right of center (Fig. 1). Inside the frame, the lever box occupied one of two positions, 3.5° left of center or 3.5° right of center. On each trial the frame and target were positioned in darkness during the intertrial interval. Then a computer-controlled shutter opened for one second. Stray light from the projected frame made the screen and the levers visible as well. As soon as the shutter closed, the subject could jab the target or verbally indicate its position in complete darkness. Responses were recorded by the computer on an absolute scale (lever 1, 2, 3, 4, or 5).

5.1.3. Procedure

5.1.3.1. Cognitive measure. The two response measures were designed to access the two visual pathways selectively. For the cognitive system the subject verbally estimated the position of the target spot on the center lever. The choices were 'far left', 'left', 'center', 'fight', or 'far right', so that the response was a five-alternative forced choice. The choices were identified with the five lever positions, which were centered before the subject during the instruction period, when the screen was illuminated by general room lighting and the frame was not projected. The five levers, and nothing else, were visible when the five alternatives were defined. By equating the responses with the visible levers in the apparatus, we could assign estimations in degrees of angle to the qualitative verbal responses. Interpretation of the data depends upon presence or absence of
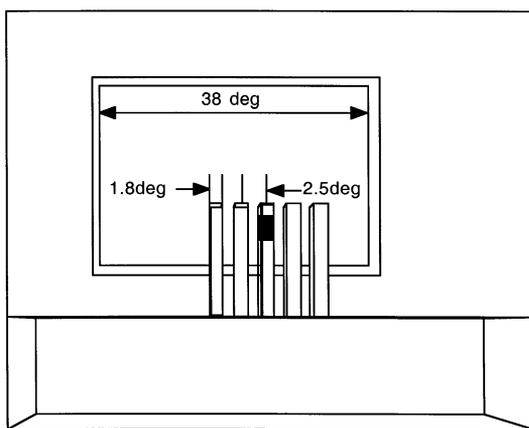

Fig. 1. Apparatus used in the verbal judging and motor jabbing experiments (not to scale). The five levers were real 3-D objects, while the background rectangle was projected through a shutter from a tungsten-halogen bulb.

Roelofs effects, however, not on absolute calibrations of the cognitive measure. In the present series of experiments the cognitive measure serves as a control to assure that a cognitive illusion is present, differentiating the cognitive and sensorimotor systems.

Subject instructions in the verbal condition emphasized an egocentric calibration. Quoting from the written instructions that were read to each subject, 'In this condition you will be telling the experimenter where you think the target is in relation to straight ahead.' Further, 'If the target looks like it's directly in front of you, you will indicate this by saying 'center''. Thus center was defined in terins of the subject's body rather than the apparatus or the frame.

5.1.3.2. Sensorimotor measure. The subject rested the right forefinger on a foam pad mounted on the centerline of the apparatus just in front of the chin rest, then jabbed the target with the forefinger as soon as the target disappeared. Thus both cognitive and sensorimotor measures were open-loop, without error feedback. Before the experimental trials began, subjects practiced jabbing the target — some were reluctant to respond vigorously at first for fear of damaging the apparatus. Subjects then received at least ten practice trials in the jab condition and ten the verbal condition.

5.1.3.3. Trial execution. A computer program randomly selected target and frame positions, with the exception that an identical set of positions could not occur on two successive trials. For verbal trials, the experimenter recorded the subject's response by typing a number (1–5) on the computer's keyboard corresponding to the subject's verbal estimate. The computer recorded motor responses automatically.

In each trial one of the two target positions and one of the three frame positions was presented, exposed for 1 s, and extinguished. Since the projected frame provided all of the illumination, target and frame exposure were simultaneous. A computer-generated tone told the subject to respond. For no-delay trials the tone sounded as the shutter extinguished the frame, while on other trials the tone began after a 1 or 2-s delay. During the delay the subject sat in darkness. Two target positions × three frame positions × two response modes × three delays resulted in 36 trial types. Each trial type was repeated ten times for each subject, resulting in a data base of 360 trials/subject. There was a brief rest and a chance to light adapt after each block of 60 trials.

Data were collated on-line and analyzed statistically off-line. Two-way ANOVAs were run for each subject, each response mode, and each delay condition. Factors were frame position and target position. Summary statistics were analyzed between subjects.
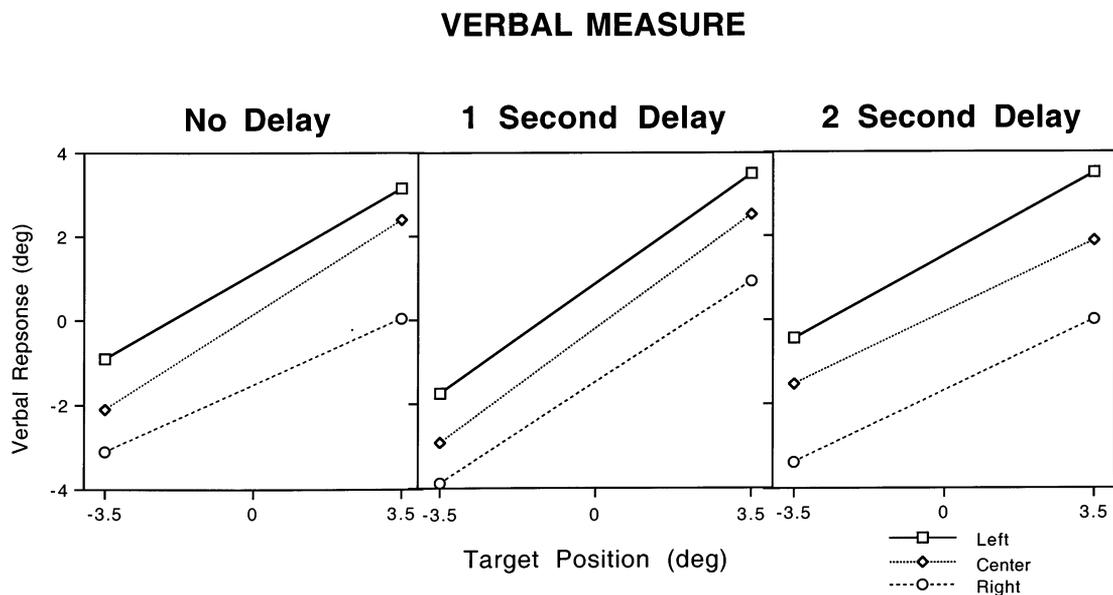
VERBAL MEASURE

Fig. 2. Mean verbal responses, used to assess the cognitive visual system, averaged across subjects. Roelofs effects, seen as separations between the diagonal lines in each panel, were significant for all conditions. The legend indicates position of the projected frame.

5.2. Results

5.2.1. Cognitive measure

The Roelofs effect, measured as a main effect of frame position, was significant under all delay conditions (Fig. 2). Subjects tended to judge the target to be further to the left than its actual position when the frame was on the right, and vice versa. In the no-delay condition six of seven individual subjects showed a significant Roelofs effect ($F(2,5) > 8.43$, $P < 0.05$), and the magnitude of the Roelofs effect averaged across subjects was 2.23° (S.E. 0.86°). In the 1-s delay condition eight of nine subjects showed a significant Roelofs effect using the same statistical criteria, and the magnitude of the effect was 2.30° (S.E. 0.86°). In the 2-s delay condition six of eight subjects showed a significant effect; the magnitude of the effect was 2.33° (S.E. 0.96°). Technical problems made data unavailable for some subjects in the no-delay and 2-s delay conditions.

5.2.2. Sensorimotor measure

In the no-delay condition, the results can best be summarized with the generalization that subjects hardly ever missed the target, regardless of target position or frame position (Fig. 3, left panel). Seven of eight subjects showed no significant Roelofs effect (frame effect $P > 0.094$). Averaged across subjects, the magnitude of the Roelofs effect was 20 min arc (S.E. 22 min arc). Performance rapidly deteriorated when a forced delay was interposed between stimulus offset and response. At 1-s delay (Fig. 3, center) there was a small but significant effect in half of the subjects ($P < 0.05$, $n = 4$), and no effect in the other half ($P > 0.228$, $n = 4$, Fig.

3, center). Average magnitude of the effect was 17 min arc (S.E. 12 min arc). At 2 s delay (Fig. 3, right) five subjects showed a significant effect ($P < 0.05$) while four did not ($P > 0.237$), for an average magnitude of 44 min arc (S.E. 12 min arc).

5.2.3. Comparison of the two measures

A separate ANOVA was run to compare the cognitive and sensorimotor conditions, using response mode as an independent variable and the magnitude of the frame effect as the dependent variable. This ANOVA showed a significant difference between cognitive and motor measures ($F_{1,43} = 12.45$, $P = 0.001$), as expected from the robustness of Roelofs effects with the cognitive measure and the absence of Roelofs effects at short delays with the motor measure.

The sizes of the Roelofs effects under various conditions can be compared by measuring the difference between average response with the target on the right and with the target on the left in Figs. 2 and 3. The cognitive measure shows a large and consistent deviation that is unaffected by delay, replicating Bridgeman et al. (1997), while the sensorimotor effect slowly grows as delay increases. At 2-s delay, the frame's influence becomes significant for the majority of subjects.

5.3. Discussion

In addition to replicating some of the results of Bridgeman et al. (1997), this experiment showed that the sensorimotor pathway maintains veridical information about target position (unaffected by visual context) for about 2 s. At 1-s delay the sensorimotor system's

behavior is similar to what it was without delay (Fig. 3); at 2 s a small but consistent Roelofs effect begins to appear, where visual context affects isomorphic motor behavior. Beyond that time Roelofs effects dominate the motor responses; by 4 s almost all subjects show significant Roelofs effects with a sensorimotor measure (Bridgeman et al., 1997).

Slopes of the verbal functions are consistently less than 1 (Fig. 2), indicating that subjects tend to perceive the target closer to the center of the array than it actually is. This effect has been observed with verbal measures in previous work both on the Roelofs effect and by others (i.e. Pagano & Bingham, 1998), and is not an artifact of the five-alternative forced-choice response method (Bridgeman et al., 1997). Since the slopes of the functions and the separation of the functions for each frame position are independent parameters, the slope does not affect the magnitude of the Roelofs effect. In fact, the Roelofs effect can be evaluated at any one frame position, so that slope is not a factor. The slopes may be less than 1 because subjects tend to fixate the target visually, and the oculomotor efference copy has a gain of less than 1. Thus eccentricity would be underestimated.

The slopes of the Roelofs functions agree quantitatively with this hypothesis. The cleanest measure of the slope of the response function, with minimal interference from eccentric frame positions or response delays, is the verbal measure with the frame centered and no response delay (Fig. 2, left panel, center data line). The slope of this line is 0.63, which can be compared to a static efference copy gain of 0.61 obtained by the technique of Bridgeman and Stark (1991). The slope is

also close to an earlier estimate of efference copy gain, calculated from data of Dichgans, Körner and Voigt (1969) to a range of 0.60–0.63 (Bridgeman, 1995). While the close agreement of slope and efference copy gains may be coincidental, the data are consistent with the hypothesis that the static efference copy gain is responsible for the slopes of the response functions with a verbal measure. In contrast, the larger slopes in the motor measure must come from sources other than efference copy alone.

6. Dissociation of cognitive and sensorimotor signals

The most rigorous way to segregate cognitive and sensorimotor representations is with double dissociation, showing one case where spatial information affects only the cognitive system and another where similar spatial information affects only the sensorimotor system (Bridgeman et al., 1981). To demonstrate a double dissociation of perceptual and sensorimotor systems in the present data, it is necessary first to determine perceived positions while motor behavior is held constant, and then to determine motor behavior while perceived position is held constant. This process is described in Figs. 4 and 5, for the zero-delay conditions.

The first step is to determine the actual target positions that would be present when the motor response is nulled. In a spatial array the definition of a null point is arbitrary, but the most neutral point is the straight-ahead direction, with the target deviating neither to the subject's left nor to the right. Thus we define the null
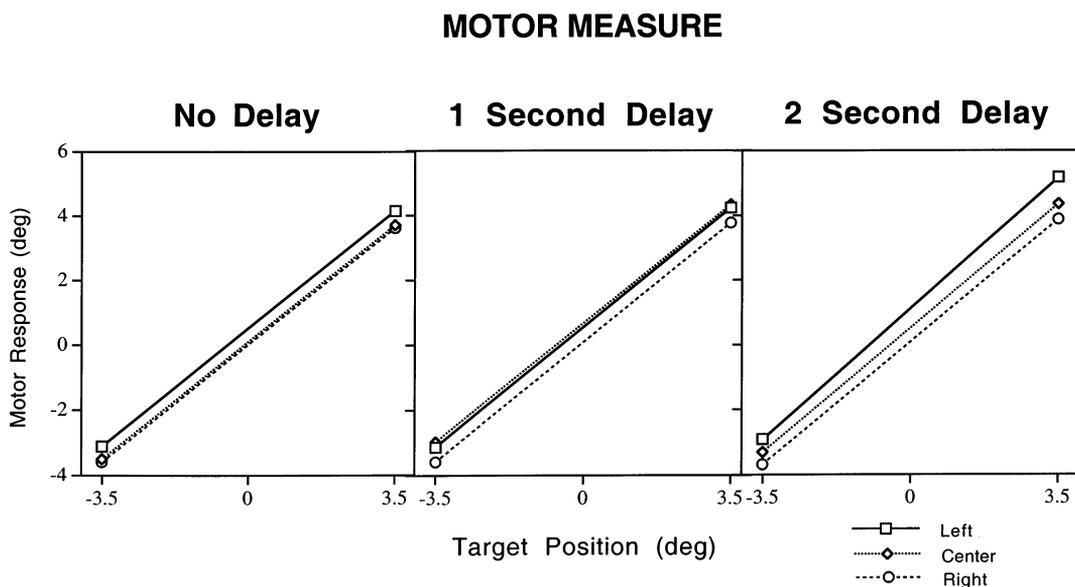
MOTOR MEASURE

Fig. 3. Mean motor responses, used to assess the sensorimotor visual system, averaged across subjects. Display format as in Fig. 2. Near-superimposition of the diagonal lines indicates that subjects were not influenced by the frame position when they jabbed the target.
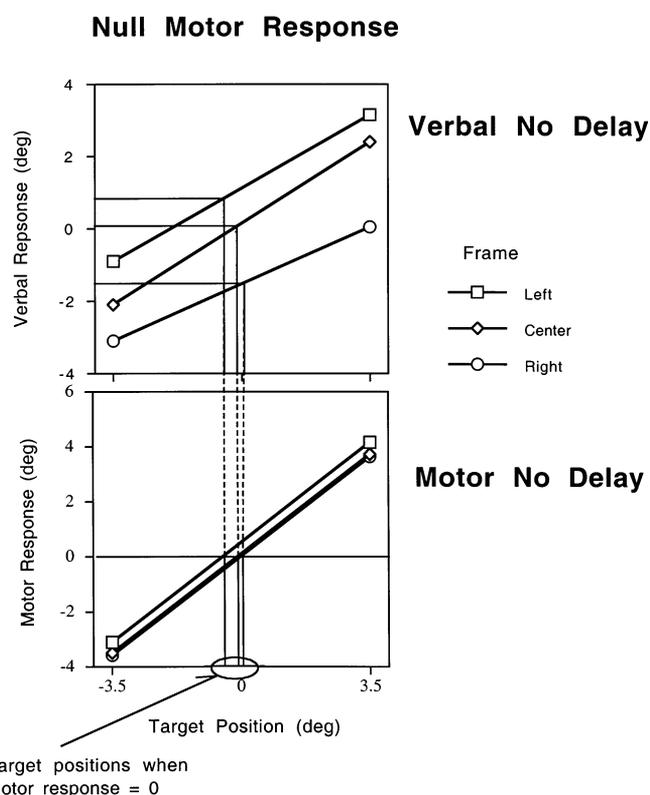
Null Motor Response

Fig. 4. Verbal response under conditions in which subjects indicate that the target is straight ahead with the motor measure. Verbal data (top) are taken from the left panel of Fig. 2, and motor data (bottom) are taken from the left panel of Fig. 3.

position as a motor jab in the straight-ahead direction. Subjects did not see trials with targets in the straight-ahead direction, but since we know from Bridgeman et al. (1997) that motor jabs to eccentric target positions predict very well the positions of jabs to targets in more central positions, we can use linear interpolation to find where subjects would jab to targets that are straight-ahead.

In Fig. 4, bottom panel, the motor data (from Fig. 3, left panel) are replotted. A horizontal line is drawn through the data at a level where the response is at zero, or straight ahead. The points where this line crosses the three data plots show target positions where subjects would jab straight ahead. Because of the lack of a Roelofs effect, the corresponding target positions are very close together for the three frame positions on the graph.

The next step is to project these three positions, representing the target positions where subjects jab straight ahead, onto the plot of the verbal data (Fig. 2, left panel). This will tell us where the subjects would have perceived tha targets to be when they jabbed at them straight ahead. Projecting the null-response lines vertically up to the verbal data (top panel), we find the points where the three target positions intersect the

verbal-condition data lines. These are at widely differing locations, because the frame biases the perceived locations in the Roelofs effect.

In the final step, the points where the jab data and the verbal data intersect are projected horizontally over to the axis on the left side of the upper graph of Fig. 4. The horizontal lines intersect the verbal response axis in locations where subjects would would perceive the targets to be when they point at them straight-ahead. They would perceive the targets in the indicated disparate positions. Thus we have nulled the motor responses and found large signal offsets in the cognitive system's spatial values.

The inverse situation is shown in Fig. 5, where the bottom panel shows the actual positions of the targets when the subject perceives them to be straight ahead (from Fig. 2, left panel). Because of the Roelofs effect, the frame's position introduces considerable variation into the actual target positions. Data analysis follows the same steps outlined for Fig. 4. When projected onto the motor responses (top panel), we see that motor responses would occur at widely varying positions (depending on frame position) for targets that are perceived to be straight ahead. Thus, nulling the verbal response position reveals large signals in the sensorimotor system. Combining this result with the one discussed in the previous paragraphs leads to a double dissociation between cognitive and sensorimotor representations of visual space (Fig. 6).

7. Experiment 2

One reason for the differences between subjects in the motor measure, with some subjects showing significant Roelofs effects and others showing no effects, might be a difference in response latency. If some subjects respond quickly, while sensorimotor pathway memory is still intact, while others respond only after memory in the sensorimotor pathway has dissipated, we might see longer response latencies in subjects who demonstrate a Roelofs effect in jabbing. To investigate these effects, we repeated the motor condition of Experiment 1 while measuring reaction time (RT). At the same time we investigated the behavioral effects of longer delays.

7.1. Method

7.1.1. Subjects

Six University of California undergraduates participated. All were right-handed and had normal or corrected-to-normal acuity.

7.1.2. Apparatus and procedures

Design of the experiment was the same as in Experiment 1 except that RT was measured by the laboratory
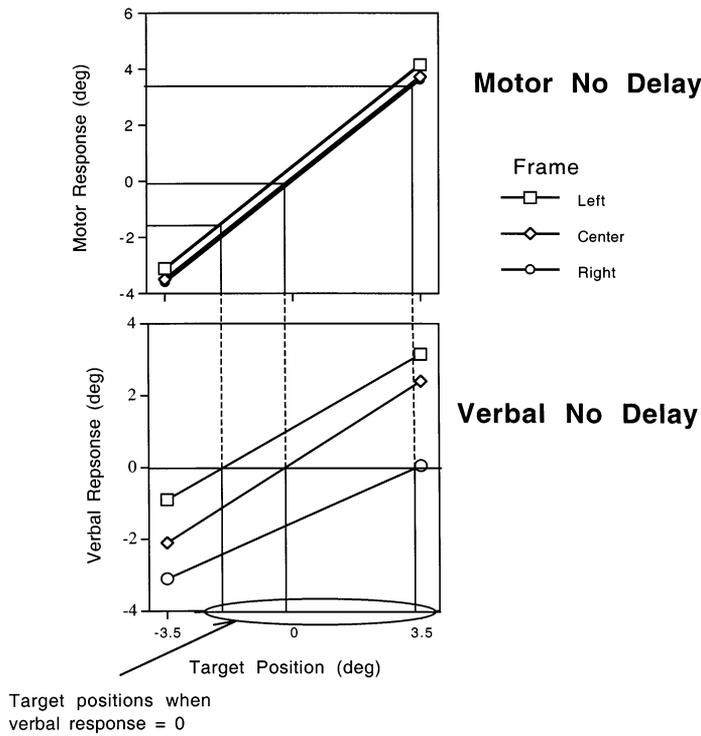
Null Verbal Response

Fig. 5. Motor response under conditions in which subjects perceive the target to be straight ahead as assessed with the verbal measure. Motor data (top) are taken from the left panel of Fig. 3, and verbal data (bottom) are taken from the left panel of Fig. 2.

computer that controls the experiments, from onset of the auditory response cue to the click of the microswitch on a response bar. The zero-delay condition was the same as in Experiment 1. Delays were increased to 2 and 4 s, the first value matching the maximum delay in Experiment 1 and the second matching the minimum delay in our previous work (Bridgeman et al., 1997). Only the motor-response condition was run.

7.1.3. Statistical analysis

RTs of less than 40 ms were rejected as anticipations. RTs of more than 1 s were rejected because they usually resulted from a subject failing to jab firmly enough to trip a response microswitch on the first try, so that the computer recorded a second try. The remaining RTs were normalized with an arcsin transformation, and each statistical test was performed once with raw data and again with transformed data. Differences in the results from the two sets of tests were negligible; only the results for transformed data are reported here. Accuracy is defined as signed error and measured as standard deviation. Since both error and reaction time are dependent variables, the relation between the two was examined with correlation techniques. Statistical techniques were otherwise identical to those of Experiment 1.

7.2. Results

7.2.1. Roelofs effect

None of the subjects showed a Roelofs effect in the no-delay condition. As delay increased there was an
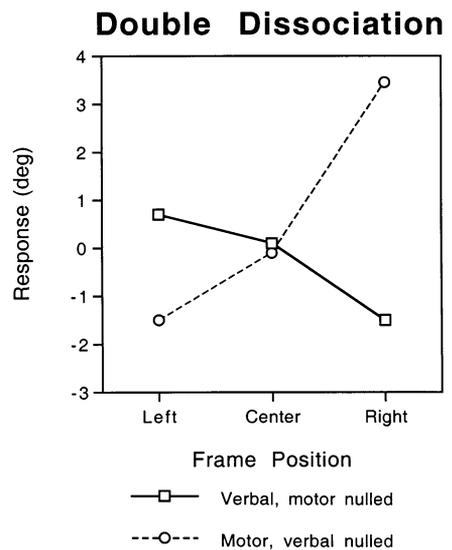

Fig. 6. Double dissociation of cognitive and sensorimotor systems, based on data replotted from Figs. 5 and 6.

increasing tendency to show a Roelofs effect; for five of the six subjects, ANOVA showed a significant effect of delay interval on the magnitude of the Roelofs effect (min. $F(2,15) = 3.75$, $P = 0.048$) with frame and delay as factors.

7.2.2. Reaction times

Mean RT was 482 ms at zero delay, 541 ms at the 2-s delay, and 551 ms at the 4-s delay. An ANOVA with factors of target position, frame position and delay showed that this increase in RT with response cue delay was significant in five of the six subjects (min. $F(2,108) = 1.95$, $P = 0.0016$ or less).

The relationship of RT to response error was analyzed at each of the three delays for each of the six subjects. Only one of the 18 resulting linear regressions was significant at $P < 0.05$, and this result can be attributed to spurious correlation. In other words, the latency of response was not related to the accuracy of that response. Reasoning that the fastest RTs test most strongly the hypothesis that faster reaction times should result in less error, we also analyzed the fastest reaction times. For each subject, the fastest RT at zero spatial error was subtracted from the fastest RT at the maximum error for the corresponding delay condition. Again, none of the differences were statistically significant (maximum $t(5) = 2.43$, $P = 0.06$). Thus even at zero response delay, where there was no bias from the Roelofs effect, response variability and RT were unrelated.

7.3. Discussion

The Roelofs effect results are consistent with Experiment 1, with longer delay times. Again the jabbing responses were insensitive to the position of the visual context at zero delay, but the context had an increasing effect as delay increased.

RT, defined as the interval between the onset of the response cue and the closing of the target's microswitch, increased as the enforced delay increased. This result could have been due to decreased vigilance after longer delays, or to greater uncertainty about the expected time of cue onset as delay increased. The weak relationship of RT to response error shows that the most accurate responses were not necessarily the fastest. Since the estimate of the duration of motor memory from Experiment 1 is about 2 s, and most RTs were in the range of 400–600 ms, the quality of spatial information available for jabbing apparently did not change significantly within the small range of variation in RT. The result also contradicts Fitts' law, which predicts greater response variability at the fastest RTs. In the zero delay condition, where Roelofs biases are not an issue, fast responses were as accurate as slow ones. A degrading sensorimotor system's memory for position

might have resulted in larger effors at longer latencies. Fitts' law predicts the reverse, a speed–accuracy trade-off. It is possible that the two effects cancelled at the level of response execution, yielding a nonsignificant result overall. Alternatively, the range of RTs may have been too small for a Fitts'-law relationship to emerge. The current method cannot test these hypotheses directly.

8. Experiment 3

We hypothesize that the cognitive representation of visual space exhibits the Roelofs effect because it specializes in pattern recognition rather than localization. In contrast, the sensorimotor representation does not show the Roelofs effect because egocentric localization is fundamental to its evolutionary function. The sensorimotor system was probed with an isomorphic task, in which there is a 1:1 relationship between the position of the target and the position of the extended finger during jabbing. No decision was necessary because only one target was displayed. The experiments required a temporal decision about when to act (triggered by the sound of the tone), but the spatial decision about where to act was trivial and always the same.

The function of the cognitive system is to make decisions about objects and events in the visual world: 'who is there', 'is that a banana', 'is it ripe', etc. In contrast, isomorphic behavior in the sensorimotor system requires no decisions about object identity. It answers questions such as 'where is that branch', 'how far is the next stepping stone', etc. Isomorphic motor behavior must be linear to be effective, while a decision represents a nonlinearity. Because the sensorimotor system has no memory, its information basis for decision-making must be very limited. Can the sensorimotor system continue to govern behavior when both a decision and an isomorphic response are required?

To explore this question, we conducted an experiment in which a judgment about which of two possible targets to jab was combined with the motor response. The Roelofs effect is again used as a marker for the use of information in the cognitive system. If the motor response remains accurate and does not show a Roelofs effect, we assume that the decision process is handled within the sensorimotor system. A Roelofs effect in the two-target condition of this experiment would suggest that the cognitive system must control behavior in tasks that require both isomorphic response and decision. In addition, subjects could not perform accurately simply by jabbing where they had fixated during the exposure period, because the chance of the last fixation being on the correct target was only 50%.
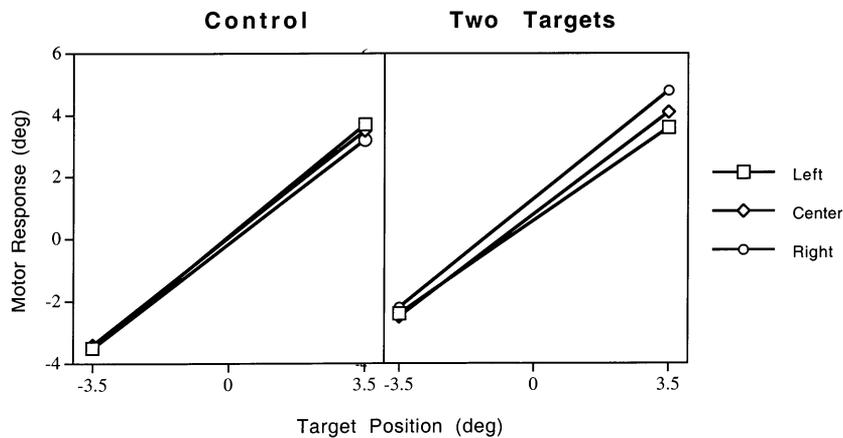
Fig. 7. Left: Jabbing performance in a control condition similar to the left panel of Fig. 3. Right: Jabbing in a condition that is similar except that two targets are present, separated by 5 deg. Graphs are corrected so that correct responses to the left target and to the right target superimpose. Subjects are able to act without systematic disturbance from the frame position, even while they are making a cognitive decision about which of the two targets to jab.

8.1. Method

8.1.1. Subjects

Four of six new subjects were from the same population as in Experiments 1 and 2. Two additional older subjects, one naive about the purpose of the study, also participated. All had normal or corrected-to-normal visual acuity.

8.1.2. Apparatus and procedure

The apparatus is the same as that used in Experiments 1 and 2, except that two targets were displayed in the decision condition. Only motor no-delay trials were run. Since errors in these trials were rare and generally small in Experiments 1 and 2, we needed only one flanking lever for each of two target levers to record errors. The second and the fourth levers became the targets, each marked with a black rectangular target area as in Experiments 1 and 2. The non-target levers (the far left, center, and far right) were white.

In the decision condition, a low-pitched or high-pitched beep sounded upon offset of the stimuli. Subjects were instructed to jab the left target if they heard a low beep, or to jab the right target if they heard a high beep. Subjects were not able to fixate the target visually because they were unaware of which stimulus would become the target until after stimulus offset. Thus, this condition tested the capacity of the internally stored sensorimotor representation.

During training, the subject was familiarized with associating a high- or low-pitched beep with each target condition. Frame and target positions were presented in pseudorandom order in each block of 60 trials for each condition. In the control condition there was only one target, on the third (center) lever, replicating the motor no-delay trials of Experiments 1 and 2.

Separate two-way ANOVAs were run for each subject and each condition (with factors target main effect, frame main effect, and interaction). The ANOVAs assessed errors, calculated as the distance of each response from the correct lever (i.e. two or four). Response time was recorded to evaluate hesitation (and thus confidence) of responses.

8.2. Results

As expected, there was no main effect of frame position (and thus, no Roelofs effect) for the one-target control condition ($F(2,30) < 3.32$, $P > 0.05$), as shown in Fig. 7, left panel.

Subjects were able to use information coded in the sensorimotor system, uninfluenced by the Roelofs effect, in the task involving both a decision and an isomorphic motor response. We found no frame effect for the two-target condition in any of the subjects (maximum $F(2,30) = 3.31$, $P > 0.05$) (Fig. 7, right panel). This finding implies that the cognitive processing involved in making a simple left-right decision does not engage the cognitive system's map of visual space, as would have been revealed by a Roelofs effect in the motor response. The range of error in the one-target condition ($\pm 0.10–0.31°$) was smaller than in the two-target condition ($\pm 0.17–1.61°$), though RTs were not significantly different.

8.3. Discussion

The finding of accurate jabbing in the one-target condition replicated Experiment 1. More important is the lack of a Roelofs effect when a choice between two similar targets is required. Independence from frame effects is a marker for the use of sensorimotor-system information. Apparently the cognitive system can in-

form the sensorimotor system about which of two possible targets to approach, and the sensorimotor system can use its own egocentrically calibrated spatial information to guide the movement.

It is not clear how this can be achieved, because the codes of the cognitive and the sensorimotor systems should be incompatible. The cognitive system's code for visual information is object-centered, with space represented as relations among visual objects. We have impressions about what is in front of us and what is to the sides, but we are frequently in error. The universality of the Roelofs effect and other context-based localization illusions in perception is evidence for this.

The sensorimotor system, in contrast, possesses an egocentric calibration that is inaccessible to perception but can be used to control visually guided behavior. In transferring information from the cognitive to the sensorimotor representation, the cognitive system would have to inform the sensorimotor system in object-relative coordinates about which bar to jab. But the sensorimotor system is insensitive to object relationships, and generates motor commands that link visually derived positions with eye or limb movements.

Eye fixation position, driven by visual attention, might enable the two incompatible codes to be linked. If the position of fixation becomes the only relevant image parameter for the sensorimotor system, visual space would collapse around that single point, and context would become irrelevant. This strategy would require either oculomotor fixation on the intended target or a planned saccade to the target, however. In our experiment the subjects did not know which target would be jabbed while they were visible, but they could have fixated on both. Experiments monitoring eye movements before and during motor action will be needed to test this hypothesis.

9. General discussion

The interpretation that our results are due to a dissociation between cognitive and sensorimotor visual systems is based on the following factors: (1) A large and consistent Roelofs effect is seen for cognitive measures at zero delay, but none is seen for sensorimotor measures. (2) With increase in response delay the sensorimotor measure changes, while the cognitive measure does not. (3) The results are consistent with psychophysical, neurophysiological and clinical data of others.

Action can be divided into three levels: eye movements, movements of body parts, and locomotion. The first level, eye movement, normally functions without conscious intervention, though some kinds of saccadic eye movements can be initiated voluntarily. As Wong and Mack (1981) showed, saccadic eye movement control can take advantage of veridical, egocentrically or-

ganized spatial information that is either currently present in the retinal input, or is used to aim saccades within a few hundred msec of stimulus offset. At longer delays, though, cognitive illusions (induced motion in this case) distort saccadic control.

The empirical work described in this paper is at the body parts level. Experiment 1 shows that information coded in this system is available for open-loop control for about 2 s; after that, cognitive information must be imported into the sensorimotor system to control behavior. Milner and Goodale (1995) describe many other characteristics of this component. Their studies concern perception or motor engagement with objects and properties of objects, such as size or orientation, while our studies concern egocentric localization of objects. The three levels are defined in terms of body parts used and the time needed to execute actions; thus, throwing or other ballistic actions belong to this level, even if their eventual result is delayed or at a distance.

The sensorimotor branch at this level is capable of veridical localization under conditions where the cognitive branch is the victim of illusions of location induced by biased visual contexts. Using a task that did not involve illusions, Pagano and Bingham (1998) demonstrated independence of errors in a perceptual and a sensorimotor task. Consistent with the characterizations of cognitive and sensorimotor systems proposed here, they find that verbal judgments are anchored to the range of experienced distances (a property requiring a memory of past trials) while the motor responses are more closely related to the information available in a single trial. Their result can be interpreted in terms of the present two-visual systems hypothesis, but it can also be interpreted as a difference in task-specific organizations. Deciding between these two interpretations requires analysis of the present results and the neurological literature on the effects of parietal versus temporal lesions.

Decisions about what to do, even in a motor task, normally originate from the cognitive branch. Objects of intended action are selected in the cognitive system, yet accurate isomorphic action is still possible based on information held in the sensorimotor system.

The locomotion level will not be reviewed in detail here, because it is not directly addressed by the current experiments. This level is isolated in studies where subjects can interact with a visual environment only through locomotion, walking or climbing through it. For example, perception of distance on the order of meters, measured by having subjects mark equal-appearing intervals, is non-linear, with large errors. But when subjects walk to a target, they do so accurately (Loomis, DaSilva, Fujita, & Fukusima, 1992). When another target was placed twice as far away as the original one, subjects walked twice as far, despite their distorted perceptual judgments. This experiment ex-

pands and formalizes a common experience: one can ask a person to judge a distance to a target by any measure (number of arm spans, meters, etc.) and receive wildly erroneous estimates. But when asked to walk to the same target, the same person does not suffer from the verbally obtained distortions.

Recent experiments have shown that the locomotor system's accurate spatial map, like that in our pointing and jabbing experiments, has a limited memory. Proffitt, Bhalla, Gossweiler and Midgett (1995) have found that subjects greatly overestimate the steepness of a hill with verbal estimates, but are much more accurate if asked to adjust a tilt board to match the slope. After a delay, however, the tilt-board estimate is significantly steeper, in the direction of the cognitive overestimate. So again it seems that after a delay the cognitive system informs isomorphic motor responses as well as verbal judgments. Here, however, motor estimates remain accurate for at least a few minutes following termination of exposure to the stimulus situation.

A few consistent rules apply to all three of these components of the sensorimotor branch of vision. All three show an initial response that is more veridical than the corresponding cognitive measures, and all begin to show errors in the direction of cognitive measures after a delay. The critical delay in each system seems to correspond closely to the amount of time required to execute a meaningful interaction with the world in the corresponding motor output modality; on the order of hundreds of msec for saccade control, seconds for arm and head movements (Jakobson & Goodale, 1991 and the present results), and minutes for hill-climbing or other locomotion. Each component seems to hold information long enough to act on it, but no longer. In each case, cognitive information can coexist with contradictory motor information in the nervous system without apparent conflict, showing the need for a segregation of the cognitive and sensorimotor representations. And in each case, not only visual direction but other aspects of the world must be encoded accurately as well.

The two-visual-systems interpretation can help to organize the large literature on spatial orientation; we need not expect studies measuring cognitive-system capabilities to show results consistent with studies measuring sensorimotor-system capabilities, or vice-versa. Many studies of locomotion, for example, relate to a sensorimotor branch of locomotor control, without necessarily invoking a perceptual role in adjusting locomotor behavior to current conditions. Rieser, Pick, Ashmead, and Garing (1995) measured adaptation of locomotor behavior after exposure to various feedback gains between locomotion and optic field flow under naturalistic conditions; the measure is entirely within the sensorimotor system. The dependent measure, open-loop walking to a target, meets the conditions that we defined above as necessary to access a sensorimotor representation: immediate testing, motor execution, and behavior isomorphic to a stimulus. The result does not contradict the lack of memory found in our study, because Rieser et al. measured a parametric change rather than an episodic memory about a particular stimulus object.

Other studies relate to perception of heading by measures that are not isomorphic to the stimulus, and do not directly engage sensorimotor capabilities as defined in this paper (Cutting, Vishton, Flüchiger, Baumberger, & Gerndt, 1997; Wang & Cutting, 1999). In these studies the subjects experience an optic flow field, and judge the direction of their simulated passive locomotion. The response is symbolic rather than isomorphic to a heading, defining a cognitive-system activity in our terms.

The cognitive/sensorimotor distinction can also clarify contrasts of response methods that come from other research traditions. Brungart, Rabinowitz and Durlach (2000) compare four methods of indicating locations of nearby objects: a direct-location method with an isomorphic pointer, two methods pointing to a model of the target space, and a verbal method. In our interpretation the direct method probes the sensorimotor system, while the other three methods probe the cognitive system because there is no isomorphism between stimulus position and motor action. Indeed, the direct method was relatively unbiased and more accurate than the other methods, consistent with our results.

In some experimental designs and patterns of results, double dissociation cannot prove the presence of two underlying processes (Dunn & Kirsner, 1988). Our results differ from these conditions in several ways. First, the motor results in Experiment 1 at no delay and at 1 s delay show no Roelofs effect, juxtaposed with a substantial effect in the cognitive measure. Thus the two measures are not correlated — knowing the motor response with a given frame position does not aid in predicting what the verbal response will be, because the motor response is the same regardless of frame position. Further, the stimulus conditions are identical for the two measures, with only the response mode changing. The crossing of the two lines in Fig. 6 shows that range nonlinearities in a single representation cannot account for the result.

In conclusion, our results are consistent with the results cited above in psychophysical investigations, neurophysiological studies and neurological patients, suggesting that the most parsimonious theoretical interpretation of our results is in terms of two distinct representations of visual space in normal humans. Information storage in the sensorimotor system lasts about 2 s for limb movements, motor performance is unrelated to small differences in reaction times, and

sensorimotor system information is available to control an action triggered by a cognitive choice.

References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685.

Brenner, E., & Smeets, J. B. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, *111*, 473–476.

Bridgeman, B. (1991). Separate visual representations for perception and for visually guided behavior. In S. R. Ellis, *Pictorial communication in virtual and real environments* (pp. 316–327). London: Taylor & Francis.

Bridgeman, B. (1995). Extraretinal signals in visual orientation. In W. Prinz, & B. Bridgeman, *Handbook of perception and action. Perception*, vol. 1 (pp. 191–223). London: Academic Press.

Bridgeman, B., Kirch, M., & Sperling, A. (1981). Segregation of cognitive and motor aspects of visual function using induced motion. *Perception and Psychophysics*, *29*, 336–342.

Bridgeman, B., Lewis, S., Heit, G., & Nagle, M. (1979). Relation between cognitive and motor-oriented systems of visual position perception. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 692–700.

Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics*, *59*, 456–469.

Bridgeman, B., & Stark, L. (1991). Ocular proprioception and efference copy in perception and visually guided behavior. *Vision Research*, *15*, 1903–1913.

Brungart, D., Rabinowitz, W., & Durlach, N. (2000). Evaluation of response methods for the localization of nearby objects. *Perception and Psychophysics*, *62*, 48–65.

Cutting, J. E., Vishton, P. M., Flüchiger, M., Baumberger, B., & Gerndt, J. D. (1997). Heading and path information from retinal flow in naturalistic environments. *Perception and Psychophysics*, *59*, 426–441.

Daprati, E., & Gentilucci, M. (1997). Grasping an illusion. *Neuropsychologia*, *35*, 1577–1582.

Dichgans, J., Körner, F., & Voigt, K. (1969). Vergleichende Skalierung des afferenten und efferenten Bewegungssehens beim Menschen: Lineare Funktionen mit verschiedener Anstiegssteilheit. *Psychologische Forschung*, *32*, 277–295.

Dunn, J. C., & Kirsner, K. (1988). Discovering functionally independent mental processes: the principle of reversed association. *Psychological Review*, *95*, 91–101.

Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*, 122–136.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research*, *86*, 199–208.

Lacquaniti, F., Perani, D., Guigon, E., Bettinardi, V., Carrozzo, M., Grassi, F., Rossetti, Y., & Fazio, F. (1997). Visuomotor transformations for reaching to memorized targets: a PET study. *Neuroimage*, *5*, 129–146.

Loomis, J., DaSilva, J., Fujita, N., & Fukusima, S. (1992). Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 906–921.

Marotta, J. J., DeSouza, J. F., Haffenden, A. M., & Goodale, M. A. (1998). Does a monocularly presented size-contrast illusion influence grip aperture? *Neuropsychologia*, *36*, 491–497.

Milner, D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Pagano, C., & Bingham, G. (1998). Comparing measures of monocular distance perception: Verbal and reaching errors are not correlated. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1037–1051.

Paillard, J. (1987). Cognitive versus sensorimotor encoding of spatial information. In P. Ellen, & C. Thinus-Blanc, *Cognitive processes and spatial orientation in animal and man*. Dordrecht, Netherlands: Martinus Nijhoff Publishers.

Paillard, J. (1991). Motor and representational framing of space. In J. Paillard, *Brain and space*. Oxford: Oxford University Press.

Pribram, K. H. (1971). *Languages of the brain*. Englewood Cliffs, NJ: Prentice Hall.

Proffitt, D. R., Bhalla, M., Gossweiler, R., & Midgett, J. (1995). Perceiving geographical slant. *Psychonomic Bulletin and Review*, *2*, 409–428.

Rieser, J., Pick, H. L., Ashmead, D., & Garing, A. (1995). Calibration of human locomotion and models of perceptual-motor organization. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 480–497.

Roelofs, C. (1935). Optische Localisation. *Archives für Augenheilkunde*, *109*, 395–415.

Schneider, G. E. (1969). Two visual systems. *Science*, *163*, 895–902.

Trevarthen, C. (1968). Two mechanisms of vision in primates. *Psychologische Forschung*, *31*, 299–337.

Wang, R. F., & Cutting, J. E. (1999). Where we go with a little good information. *Psychological Science*, *10*, 71–75.

Wong, E., & Mack, A. (1981). Saccadic programming and perceived location. *Acta Psychologica*, *48*, 123–131.